

Two new sibling species of *Mantidactylus cornutus* from Madagascar

(Amphibia, Anura, Ranidae)

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A review of the Malagasy frogs which in the past were subsumed under the name *Mantidactylus redimitus*, together with new field data, led to the confirmation of the specific validity of *M. cornutus* and to the recognition of two new species: *M. tschenki*, spec. nov. from Ranomafana is morphologically similar to *M. cornutus* but shows distinct differences in advertisement call and has a slightly bilobed (instead of a roundish) subgular vocal sac. *M. tandroka*, spec. nov. from higher elevations of the Marojezy massif is distinguished by a wide head, distinct dorsal ridges, and colouration from *M. cornutus*, *M. tschenki*, and *M. redimitus*. The discovery of close syntopy of *M. redimitus* and *M. cornutus* in central eastern Madagascar confirms that they represent valid species and that advertisement calls are good indicators for specific distinctness in Malagasy anurans.

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Introduction

During the last decades it has become evident that the analysis of advertisement calls is crucial to understand the species diversity of anurans (e.g. Passmore & Carruthers 1995). This is especially true for tropical anuran communities like those in Madagascar which are poorly studied and where numerous new amphibian species are still to be discovered and described. A significant percentage of the recently discovered new species are morphologically similar to already known species and some of those sibling species pairs are hardly distinguishable when preserved (Glaw & Vences 2000). However, in all cases in which anurans with relevant differences in their advertisement calls have been investigated genetically, relevant genetic distances – indicative of reproductive isolation at the species level – have been found (pers. obs. in more than 20 species pairs from Madagascar, South America, and Asia).

In the present paper we review a complex of species in the Malagasy genus *Mantidactylus* which previously (Guibé 1978, Blommers-Schlösser & Blanc 1991) were all subsumed under the name *Mantidactylus redimitus*. Glaw & Vences (1992b) noted the bioacoustic and morphological differences of low-altitude *M. redimitus* specimens and those of mid-altitude localities, and described the latter as new species *M. cornutus*. We here provide evidence that *M. cornutus* populations as listed in the distribution map of Glaw & Vences (1994) are still composed of various species: one new sibling species was discovered during a bioacoustic survey near the village Ranomafana in south-eastern Madagascar; its morphology is very similar to *M. cornutus* but its advertisement calls are rather different. In contrast, specimens from the Marojezy massif in north-eastern Madagascar differ by distinct morphological features and are described as second new species, although their advertisement calls are not yet known.

Materials and methods

Vocalizations were recorded using portable tape recorders with an external microphone (Vivanco EM 238) and were analyzed with the MEDAV sound analyzing system Spekro 3.2. The following morphological measurements were taken with a calliper to the nearest 0.1 millimeter: SVL (snout-vent length), HW (head width), HL (head length), ED (horizontal eye diameter), END (eye-nostril distance), NSD (nostril-snout tip distance), NND (nostril-nostril-distance), TD (horizontal tympanum diameter), HAL (hand length), FORL (forelimb length), HIL (hindlimb length), FOL (foot length), FOTL (foot length including tarsus), IMTL, IMTH (length and height of inner metatarsal tubercle), T1L (length of first toe). Webbing formula is given according to Blommers-Schlösser (1979). Institutional abbreviations are as follows: BM (Natural History Museum, London); MNHN (Muséum national d'Histoire naturelle, Paris); MRSN (Museo Regionale di Scienze Naturali, Torino); ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn); ZSM (Zoologische Staatssammlung, München). Statistical analyses were carried out using SPSS for Windows, version 9. We performed Mann-Whitney U-tests to test significance of intersexual differences in size and morphometric ratios (relative tympanum length, ratio TD/SVL; relative size of inner metatarsal tubercle, IMTL/SVL and IMTH/SVL). Temporal and metric measurements are given as range, with mean \pm standard deviation in parentheses.

Results

Mantidactylus redimitus (Boulenger, 1889)

Material examined. BM 1947.2.26.55 (holotype; original number BM 89.8.1.24; Madagascar); BM 92.3.7.39-41 (Sahembendrana); BM 1928.5.9.11-12 (Brickaville); BM 1988.593 (Ambatovaky); MNHN 1973.911 (Marojezy, 600-1300 m altitude); MNHN 1973.937 (Marojezy, 300 m altitude); MNHN 1973.938-939, 1973.941 (Marojezy, 600 m altitude); ZFMK 52704-52705 (Nosy Boraha); ZFMK 52716 (Nosy Mangabe, juv.); ZFMK 60073 (An'Ala).

Morphology. Summarizing measurements of the specimens in Table 1 (only adults considered; type not included due to bad state of preservation) results in a male SVL of 43.4-52.8 mm (47.6 ± 3.7 mm, $n=6$) and a female SVL of 48.1-48.3 mm ($n=2$). Mean male SVL was 99% of mean female SVL. Sexual size dimorphism was not significant (U-test, $P=1$). All specimens corresponded to the description in Glaw & Vences (1994) in having short legs (tibiotarsal articulation reaching at least to the anterior eye corner, at most between nostril and snout tip), and a rather smooth dorsal skin, without large dermal spines on the eyes, and with a pair of only faintly expressed tubercles between the eyes. Mean relative tympanum size did not differ significantly between sexes (U-test, $P>0.6$), while intersexual differences in relative length and height of inner metatarsal tubercle (means of both values larger in males) were close to significance (U-test, $P=0.07$). In contrast to the following species, the femoral glands in male *M. redimitus* were prominent and always well visible. Their size was 9.7×2.9 mm in MNHN 1973.911, 8.6×2.9 mm in MNHN 1973.937, 7.8×3.0 mm in ZFMK 52704, 8.4×3.3 mm in ZFMK 52705, and 9.2×3.1 mm in ZFMK 60073.

Habitat and habits. Calling activity generally started at dusk, but sometimes single calls were also heard since the early afternoon (14.30 h). Calling males were found in February and March sitting horizontally in the vegetation (1-2 m above the bottom) along larger brooks (broader than 1 m). At An'Ala, where *M. redimitus* was observed calling syntopically with *M. cornutus*, the former was only found at the edge of a broad brook (>3 m) whereas the latter was sitting along a small afflux (not broader than 0.5 m) only several metres apart. W. Herwig (pers. comm.) photographed a specimen of *M. redimitus* at Vohidrazana on 16 July 2000 at 19.30 h. It was sitting on a leaf of a bush about 160 cm above the bottom. This record indicates that *M. redimitus* is also active in the comparatively cold and dry winter season.

Advertisement calls. Calls were recorded at An'Ala (on 11 February 1995, 17.30 h, at 22 °C air temperature) and Marojezy (on 22 February 1995, ca. 21.00 h, at 25 °C air temperature). They consisted either of single notes or note series. Each note (Fig. 1) corresponded to one expiration. At An'Ala, note duration was 274-352 ms (309 ± 22 ms, $n=9$), duration of intervals between notes was 484-717 ms (584 ± 75 ms, $n=8$). Each note was composed of 4-6 pulse groups, each of which contained 2-7 pulses. The longest note series recorded consisted of 12 notes and had a note repetition rate of 1.1/s. Frequency was 900-1400 Hz. At Marojezy, note duration was 315-350 ms (329 ± 10 ms, $n=9$), duration of intervals between notes 493-737 ms (597 ± 106 ms, $n=6$). Each note consisted of 7-10 pulse groups, each of which

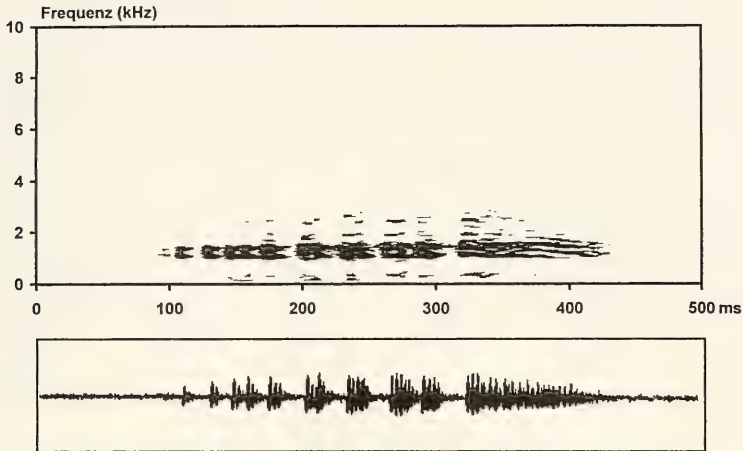


Fig. 1. Sonogram and oscillogram of one note of *Mantidactylus redimitus* from Marojezy.

contained 1-10 rather indistinct pulses. Frequency was 900-1500 Hz.

Further recordings from Nosy Boraha were analyzed by Glaw & Vences (1992a,b). The high note repetition rate (up to 2.5/s) in these recordings differ from the An'Ala and Marojezy data, and may be due to an exceptional motivation of the corresponding specimen (several specimens were calling rather close to each other). The low note duration (ca. 100 ms) as given by Glaw & Vences (1992b), however, is an artefact of analysis (probably originated by measuring note duration on the sonogram), the actual note duration in the Nosy Boraha recordings was similar to that in An'Ala and Marojezy as we ascertained by re-analysis.

Distribution. Data presented here confirm that *M. redimitus* is primarily a low-altitude species. At Marojezy, it has mainly been found at 300-600 m above sea level, only one specimen comes from an imprecise higher altitude (600-1300 m). The collecting localities at Nosy Boraha and Nosy Mangabe were close to sea level (<100 m altitude), whereas that of An'Ala was at 840 m above sea level. Sahembendrana is also at mid-altitude, while Ambatovaky and Brickaville can be considered as low-altitude sites. Beside these localities, Glaw & Vences (1994) list one additional locality, Maroantsetra-Antalaha (that means the path between both cities), which is based on personal observations in 1987 (only photographic voucher available). A further photographic record was made by W. Herwig at Vohidrazana some 700 m above sea level.

Raxworthy & Nussbaum (1996) reported *M. redimitus* [*M. redimitis* (sic!)] from altitudes of 650-1700 m in the Andringitra massif but did not list *M. cornutus*. Since *cornutus*-like specimens are known from Andringitra (see below), it is possible that this record is based on a misidentification. The same regards their record of *M. redimitus* from Ranomafana (900-1050 m altitude) which possibly refers to the new species *M. tschenki* described below. Two additional records of *M. redimitus* exists for the "Réserve Spéciale du Pic d'Ivohibe" (1200 m altitude) and the corridor to the "Parc National d'Andringitra", 900 m altitude (Raselimanana 1999). Since *M. cornutus* is not mentioned in this paper and MNHN material from Pic d'Ivohibe is *cornutus*-like these records are also likely to refer to *M. cornutus* or *M. tschenki*.

Mantidactylus cornutus Glaw & Vences, 1992

Material examined. ZFMK 52702-52703 (paratypes, Andasibe); ZFMK 53691 (holotype, Andasibe); ZFMK 59867 (Andasibe); ZSM 573/1999 (paratype, Andasibe, originally ZFMK 53690); ZSM 308/2000 (Vohidrazana, 18°57' 57" S, 48°30' 37" E, 730 m above sea level).

Notes on the type material. In the original description of *M. cornutus* (Glaw & Vences 1992b: 272) the paratypes were defined as follows: "Three adult males (ZFMK 53690, 52702, 52702) from Andasibe ...". The latter number was a typing error and must be corrected to 52703.

Tab. 1. Morphometric measurements (all in mm) of specimens of *Mantidactylus redimitus*, *M. cornutus*, *M. tschenki*, and *M. tandroka*. For abbreviations of measured variables, see Materials and Methods; further abbreviations used: M, male; F, female; SA, subadult; HT, holotype; PT, paratype; TT, point reached by tibiotarsal articulation when adpressed along the body: 0, anterior eye margin; 1, between eye and nostril; 2, nostril; 3, between nostril and snout tip; 4, snout tip; 5, beyond snout tip; 6, widely beyond snout tip.

Catalogue Nr.	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	IMTL	IMTH	TL1	TT
<i>M. redimitus</i>																		
BM 1947.2.26.55 (HT)	M	47.4	15.6	18.0	2.6	4.9	5.5	2.9	4.4	28.5	13.7	73.1	33.1	22.4	2.2	1.6	3.7	0
MNHN 1973.911	M	50.5	17.0	19.3	3.1	5.4	6.1	2.6	4.0	29.8	15.2	80.6	39.4	26.4	2.9	2.3	5.5	0
MNHN 1973.937	M	52.8	17.7	20.3	3.3	5.7	6.1	2.7	4.3	32.7	15.7	83.8	39.7	27.3	2.8	2.1	5.3	0
MNHN 1973.938	F	48.3	15.8	18.7	2.8	5.8	5.5	2.5	4.0	29.6	15.1	88.4	39.2	25.0	2.0	1.1	4.8	2
MNHN 1973.939	M	48.4	15.6	18.0	2.7	5.3	5.2	3.2	4.4	30.4	14.9	81.4	37.9	26.0	2.7	2.0	5.2	1
MNHN 1973.941	F	48.1	15.8	18.8	2.6	6.0	5.6	2.7	3.7	29.0	14.7	86.8	38.2	25.5	2.2	1.2	5.6	1
ZFMK 52704	M	44.0	15.7	17.6	2.6	4.5	5.4	3.0	4.4	26.5	12.2	67.0	31.0	20.7	2.2	1.6	3.2	1
ZFMK 52705	M	43.4	15.0	19.0	2.5	5.5	5.2	2.2	4.1	27.7	13.3	70.9	32.1	22.0	2.0	1.7	3.5	1
ZFMK 60073	M	46.6	15.7	18.0	2.5	5.5	6.0	3.0	4.1	29.2	14.2	78.2	34.2	24.0	2.8	1.9	4.3	3
<i>M. cornutus</i>																		
ZFMK 52702 (PT)	M	37.5	12.8	14.5	2.1	4.6	4.1	2.2	3.2	23.9	11.8	70.2	30.2	20.1	1.7	1.6	3.7	5
ZFMK 52703 (PT)	M	39.4	12.7	15.0	2.0	4.5	5.0	1.9	3.5	24.7	12.0	67.7	29.8	19.4	1.6	1.4	3.6	3
ZFMK 53691 (HT)	M	39.7	12.4	14.7	2.0	4.7	4.1	2.2	3.7	23.7	11.2	67.7	29.3	20.0	1.9	1.7	3.7	5
ZFMK 59867	F	38.9	12.3	14.7	2.5	4.7	4.0	2.2	3.6	24.9	11.6	73.2	31.2	20.3	1.4	0.9	3.8	6
ZSM 573/1999 (PT)	M	40.1	13.2	15.7	2.3	4.2	4.8	2.2	3.5	24.6	12.6	69.5	30.8	21.0	1.6	1.5	3.4	5
ZSM 308/2000	F	33.3	11.0	13.4	2.3	4.1	4.0	2.1	2.8	23.2	10.3	72	32.2	20.3	1.3	0.5	3.3	6
<i>M. tschenki</i>																		
MRSN A379 (PT)	M	34.7	11.0	13.0	2.1	4.0	3.7	1.7	2.9	21.6	10.4	58.1	26.1	18	2.2	1.1	–	1
ZFMK 62296 (PT)	M	36.2	12.6	14.0	2.1	4.3	3.9	2.0	3.2	26.0	12.0	67.0	29.0	20.0	2.0	1.4	3.3	6
ZFMK 62297 (PT)	M	34.8	12.2	14.0	2.2	4.5	4.2	2.0	2.8	23.7	10.7	63.5	29.2	19.4	2.0	1.5	3.2	6
ZSM 936/2000 (HT)	M	36.1	12.0	13.6	2.0	4.6	3.9	2.2	3.2	24.8	11.6	67.0	29.4	20	2.0	1.3	3.4	6
<i>M. tandroka</i>																		
MNHN 1973.912 (PT)	F	43.2	14.9	16.4	2.9	5.1	4.1	2.5	4.6	29.2	13.9	81.8	36.2	24.2	1.3	0.9	4.4	6
MNHN 1973.922 (PT)	M	38.9	13.1	14.5	2.2	4.8	3.4	2.2	3.7	26.6	13.0	74.4	32.8	21.8	1.8	1.3	4.6	5
MNHN 1973.924 (HT)	M	38.7	13.2	14.6	2.4	4.8	3.5	1.9	3.9	26.0	12.7	70.2	32.9	21.9	1.8	1.5	4.4	5
MNHN 1973.926 (PT)	F	44.7	15.3	16.7	2.8	5.4	4.4	2.5	4.2	28.8	14.5	84.1	37.6	24.5	1.5	0.8	4.8	5
MNHN 1973.927 (PT)	M	38.8	14.0	15.6	2.4	5.1	3.8	2.3	3.5	26.3	12.7	73.3	32.8	21.9	1.9	1.4	4.5	5
MNHN 1973.928 (PT)	F	39.8	13.3	14.8	2.2	5.1	3.8	2.3	3.8	25.8	12.6	78.4	34.3	22.4	1.2	1.1	5.1	6
MNHN 1973.929 (PT)	M	38.8	13.1	15.0	2.4	5.2	3.8	2.4	4.1	23.3	12.5	73.5	31.7	22.1	1.8	1.7	4.5	5
MNHN 1973.930 (PT)	SA	33.9	11.6	13.0	2.4	4.3	3.4	1.9	3.6	23.8	11.1	72.3	32.3	20.0	1.2	0.6	4.6	6
ZFMK 59894 (PT)	F	39.6	15.0	16.5	2.3	5.4	4.3	2.7	4.7	27.0	13.6	80.1	36.0	23.1	1.2	0.7	4.6	6
ZSM 937/2000 (PT)	F	41.5	15.3	16.6	2.3	5.6	4.3	2.6	4.3	28.3	14.0	85.0	38.1	24.3	1.8	0.9	4.1	6
Determination uncertain																		
MNHN 1953.74	F	37.9	11.8	14.0	2.4	4.7	4.0	2.7	3.4	25.9	13.3	76.1	33.6	21.3	1.3	0.6	3.7	5
MNHN 1991.2940	F	42.6	13.5	16.0	2.4	5.3	4.7	2.3	3.2	24.8	12.8	74.4	33.4	20.5	1.3	0.6	4.0	4
MNHN 1991.2941	M	38.8	12.3	13.9	2.1	4.7	4.1	1.8	3.6	25.5	13.0	66.3	28.6	19.4	2.2	1.6	3.2	5
MNHN 1972.571	F	39.4	12.3	14.8	1.8	4.1	4.1	2.2	3.4	–	12.9	71.5	31.6	21.8	1.3	0.6	4.0	5
MNHN 1972.572	F	35.9	12.0	14.6	2.0	3.3	4.4	2.3	3.2	–	11.6	68.2	30.9	21.0	0.9	0.4	4.3	5
MNHN 1972.1471	M	39.5	12.4	15.2	2.6	4.5	3.9	2.1	3.1	25.4	12.0	68.1	29.2	20.0	2.1	1.6	3.6	5
MNHN 1972.1472	M	41.4	13.2	16.2	2.2	4.9	4.5	2.1	3.2	24.0	11.9	68.8	29.9	20.7	1.7	1.6	4.3	2
ZFMK 50593 (PT <i>cornutus</i>)	F	40.7	13.0	14.9	2.5	4.4	4.4	2.0	3.3	24.7	12.9	74.7	33.9	22.0	1.5	0.8	3.3	6

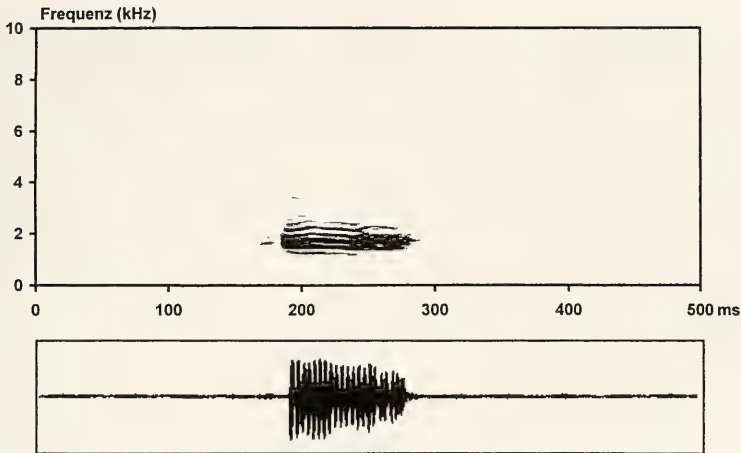


Fig. 2. Sonogram and oscillogram of one note of *Mantidactylus cornutus* from An'Ala.

Morphology. In the studied sample (see Table 1 for measurements), SVL was 37.5-40.1 mm (39.2 ± 1.2 mm, $n=4$) in males and 33.3-48.9 mm (36.1 ± 4.0 mm, $n=2$) in females. Mean male size was 109 % of mean female size, no significant sexual size dimorphism was found (U-test, $P>0.2$). All specimens largely corresponded to the descriptions of Glaw & Vences (1992b, 1994) in having rather long legs (tibiotarsal articulation reaching at least nostril, mostly beyond snout tip) and a distinct pair of blackish tubercles between the eyes. Neither relative tympanum size (mean value smaller in males) nor relative length and height of inner metatarsal tubercle (means of both values larger in males) were significantly different between sexes (U-test, $P>0.05$), but the latter may be due to small sample size.

Habitat and habits. Calling males were found in all months from December to March, indicating a prolonged mating activity during the rainy season. They were sitting horizontally in the vegetation (1.5-2.5 m above the bottom) along very small (mostly smaller than 0.5 m in diameter) and slowly running brooks, in pristine or degraded forest.

Advertisement calls. Calls were recorded at An'Ala (on 21 March 1995 at 22 °C air temperature) and Andasibe (on 16 January 1995, 19.00 h). They were long-lasting regular note series (up to several minutes). Notes (Fig. 2) were unharmonious. At An'Ala, note duration was 90-113 ms (99 ± 7 ms, $n=32$), duration of intervals between notes was 616-1280 ms (825 ± 140 ms, $n=31$), note repetition rate was ca. 1/s. One analyzed note consisted of 20 pulses and had a pulse repetition rate of 227/s. Frequency was 1150-2500 Hz, dominant frequency 1400-1950 Hz. At Andasibe, note duration was 93-111 ms (102 ± 6 ms, $n=10$), duration of intervals between notes was 536-903 ms (720 ± 131 ms, $n=9$), note repetition rate was ca. 1.3/s. One note was composed of ca. 23 pulses. Frequency was 1000-5100 Hz, dominant frequency 1300-2100 Hz.

Distribution. The species is reliably known from Andasibe (type locality, ca. 900 m altitude), An'Ala (personal observations and call recordings, ca. 840 m altitude), and most probably from Vohidrazana (only one female specimen; no calls heard, 730 m altitude). The locality Marojezy mountains, above 1300 m altitude (Glaw & Vences 1994), refers to *M. tandroka*, which is described below. All additional records of this species (Andreone 1994, Glaw & Vences 1994, Raselimanana 1998, Raxworthy et al. 1998) are in need of confirmation (see also discussion).

Mantidactylus tschenki, spec. nov.

Figs 3-4

Types. Holotype: ZSM 936/2000 (formerly ZFMK 62298), adult male, collected along the road between Ambatolahy and Ranomafana, south-eastern Madagascar, on 28 February 1996 by F. Glaw, D. Rakotomalala and F. Ranaivojoana. – Paratypes: ZFMK 62296 and 62297, adult males, collected close to the village Ranomafana



Fig. 3. *Mantidactylus tschenki*, spec. nov. (holotype ZSM 936/2000 in life, dorsolateral view).



Fig. 4. *Mantidactylus tschenki*, spec. nov. (holotype ZSM 936/2000 in life, ventral view).



Fig. 5. Calling male of *Mantidactylus cornutus* from Andasibe.



Fig. 6. Calling male of *Mantidactylus tschenki*, spec. nov. from Ranomafana (Foto: F. Andreone)

(21°14'S, 47°26'E, ca. 550-600 m above sea level), same date and collectors as holotype. MRSN A379, adult male, collected by F. Andreone at Ranomafana.

Diagnosis. *M. tschenki*, spec. nov. is characterized as a member of the genus *Mantidactylus* by presence of femoral glands and lack of nuptial pads in males, and by its close similarity to *Mantidactylus cornutus*. *M. tschenki* can be distinguished from that species by (a) the very different advertisement calls, (b) a different shape of the inflated vocal sac in calling males (single subgular in *cornutus*, slightly bilobed subgular in *tschenki*; Figs 5-6), (c) possibly by a slightly lower body size (SVL of adult males 38-40 mm in *cornutus*, 35-36 mm in *tschenki*).

Description of the holotype

Adult male, SVL 36.1 mm. For measurements, see table 1. Body slender; head longer than wide, slightly wider than body; snout pointed in dorsal and lateral views; nostrils directed laterally, slightly protuberant, much nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region concave; tympanum distinct, elliptical (slightly higher than wide), 44% of horizontal eye diameter; supratympanic fold present, straight; tongue ovoid, distinctly bifid posteriorly; vomerine teeth distinct, in two rounded aggregations, positioned posterolateral to choanae; choanae rounded. Arms slender, subarticular tubercles single; outer and inner metacarpal tubercles present; fingers without webbing; relative length of fingers $1 < 2 < 4 < 3$, finger 2 distinctly shorter than finger 4; finger disks distinctly enlarged; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaches widely beyond snout tip; lateral metatarsalia partly connected; inner metatarsal tubercle distinct, outer metatarsal tubercle not recognizable; webbing formula between toes 1 (1), 2i (2), 2e (1), 3i (2), 3e (1.5), 4i (2.75), 4e (2.5), 5 (1). Skin on the dorsal surface smooth; back with indistinct and irregular dorsolateral folds; two distinct, slightly elevated blackish tubercles between the eyes; a number of small granules and dermal spines above the eyes; no distinct enlarged tubercles in the cloacal region; ventral skin smooth on throat, slightly granular on belly. Femoral glands very poorly delimited and very indistinct from both external and internal views; a patch of 10-15 small granules are visible from internal view.

Colour after four years in preservative rather uniformly greyish brown dorsally, with a dark brown transversal band between the eyes which encloses the pair of blackish tubercles. Limbs with rather indistinct brown crossbands. Head laterally with two narrow white stripes running from the eye to the upper lip. Ventrally cream with irregular greyish brown pattern on belly and limbs. Throat (vocal sac) greyish with a lighter mottling and one discontinuous and irregular median light stripe.

Colour in life. Colour slides are only available of the holotype ZSM 936/2000 (Figs 3-4). Dorsal colouration and upper flanks brown. Three distinct dark brown crossbands were present on femur and tibia. The iris was silvery with a reddish brown spot on its posterior edge. The pupil was horizontal. A distinct white spot between posterior edge of eye and upper lip. The venter was dirty white with brownish spots on the shoulder girdle, the ventral surface of hindlegs was brownish except for the yellowish femoral glands. The throat was marbled brown and white.

Variation. The two paratypes correspond morphologically very well to the holotype. The throat lacks a light median stripe in both specimens. Colouration of ZFMK 62297 is dorsally similar to the holotype except the darker head sides and a more distinct narrow horizontal dark brown stripe underneath the canthus rostralis and the supratympanic fold. In ZFMK 62296, a different colour pattern is present which is also known in *M. redimitus* and *M. cornutus*: A distinct beige stripe runs (on each side of the body) from the snout tip along the canthus rostralis, over the eyes, broadens as dorsolateral band along the anterior back and finally makes up the whole of the flank colour on the posterior part of the body.

Habitat and habits. Calling males were sitting at night (end of February and beginning of March) on vegetation ca. 1-2 m above the bottom. They were found in primary rain forest and in degraded vegetation as well. In at least one case no water body was recognized in the vicinity of the calling males.

Advertisement calls. Vocalizations were recorded at the type locality on 2 March 1996 at ca. 22 °C air temperature: Notes (Fig. 7) are unharmonious, distinctly pulsed and emitted in regular series. Temporal parameters were as follows: Note duration 274-335 ms (293 ± 16 ms, $n = 20$), interval duration 1018-2076 ms (1393 ± 274 ms, $n = 18$). Notes consist of 16-21 pulses (18 ± 1 , $n = 20$), the pulse rate is 58-68 (63 ± 2 , $n = 20$) per second. Frequency range is 1300-4000 Hz (dominant frequency 2500-2900 Hz, another emphasized frequency band also from 1450-1550 Hz).

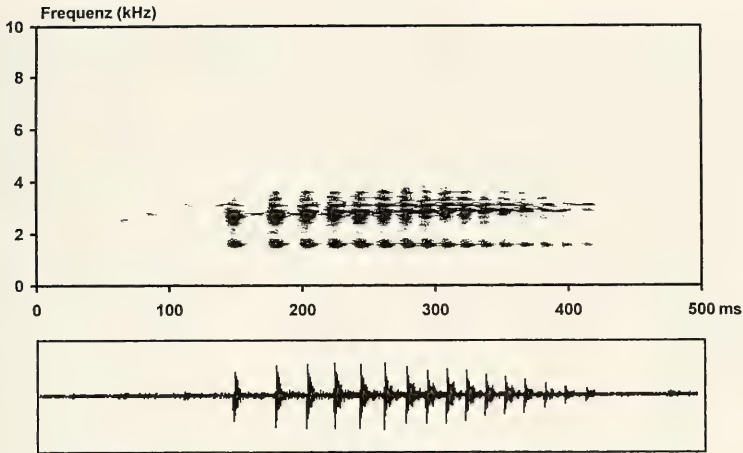


Fig. 7. Sonogram and oscillogram of one note of *Mantidactylus tschenki*, spec. nov.

Distribution. *Mantidactylus tschenki* is reliably only known from the type locality. Several additional specimens (and thus localities) possibly belong to *M. tschenki*, but a reliable attribution to either species is not possible by morphology alone (see discussion).

Etymology. *Mantidactylus tschenki* is dedicated to Michael Tschenk, in recognition of his generous support to the biosystematic research at the ZSM.

Relationships. *Mantidactylus tschenki* appears most closely related to *Mantidactylus cornutus*. Both species are very similar by their morphology.

Subgeneric attribution. *Mantidactylus tschenki* is included in the subgenus *Phylacomantis* Glaw & Vences, 1994 based on its similarity to *M. cornutus*.

Mantidactylus tandroka, spec. nov.

Figs 8-9

Types. Holotype: MNHN 1973.924, adult male, collected by Ch. P. Blanc on 2 July 1972 at the Marojezy massif, 1300 m altitude. – Paratypes: MNHN 1973.922, 1973.926-930, two adult males, three females and one subadult specimen, same collecting data as holotype. MNHN 1973.912, adult male, collected on 29 November 1972 by Ch. P. Blanc at the type locality. ZFMK 59894 and ZSM 937/2000 (formerly ZFMK 59895), two adult females, collected by F. Glaw and O. Ramilison on 28 February 1995 at Marojezy, Campsite 4 (ca. 1300 m altitude).

Diagnosis. *M. tandroka* is characterized as a member of the genus *Mantidactylus* by presence of femoral glands and lack of nuptial pads in males, and by its general similarities to *Mantidactylus cornutus*, *M. tschenki*, and *M. redimitus*. It is morphologically most similar to *M. cornutus* and *M. tschenki* but can be distinguished from these species by (a) different head proportions, with a shorter snout and a larger head width relative to SVL (see Fig. 10), (b) presence of distinct pattern of longitudinal folds on the back which is not found in any specimen of *cornutus* or *tschenki*: a pair of folds, absent in the other species, starts behind the eyes and converges on the anterior back, fading in an area enclosed by the dorsolateral folds. Some specimens of *M. tandroka* also remind the sympatric *M. leucomaculatus*; this species, however, differs by lack of the tubercle pair between the eyes (black spots may be present but are never prominent), lack of dorsal ridges, and the presence of laterally blackish vocal sacs in males.

Description of the holotype

Adult male, SVL 38.7 mm. For measurements, see table 1. Body slender; head longer than wide, wider than body; snout slightly pointed in dorsal view, truncated in lateral view; nostrils directed posterolaterally, slightly protuberant, much nearer to tip of snout than to eye; canthus rostralis distinct,



Fig. 8. Female paratype (ZSM 937/2000) of *Mantidactylus tandroka*, spec. nov. from Marojezy in life (dorsolateral view).

straight; loreal region concave; tympanum distinct, elliptical (higher than wide), 50 % of horizontal eye diameter; supratympanic fold very distinct, slightly curved; tongue ovoid, distinctly bifid posteriorly; vomerine teeth distinct, in two rounded aggregations, positioned posterolateral to choanae; choanae rounded. Arms slender, subarticular tubercles single; a paired outer and a single inner metacarpal tubercles present; fingers without webbing; relative length of fingers $1 < 2 < 4 < 3$, finger 2 distinctly shorter than finger 4; finger disks distinctly enlarged; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaches distinctly beyond snout tip; lateral metatarsalia partly connected; inner metatarsal tubercle distinct, outer metatarsal tubercle very small, almost not recognizable; webbing formula between toes 1 (1), 2i (2), 2e (1), 3i (2), 3e (1.25), 4i (2.75), 4e (2.5), 5 (1). Skin on the upper surface smooth; back with many irregular smaller folds, arranged as a discontinuous network; a pair of distinct folds runs from behind the eyes, converge centripetally onto the anterior back, curves slightly towards the flanks and fades; laterally from these, a pair of dorsolateral folds runs from ca. 4 mm behind the supratympanic fold to the inguinal region. Two distinct, blackish tubercles between the eyes; a number of granules and small dermal spines above the eyes; no distinct enlarged tubercles in the cloacal region; ventral skin slightly granular on belly, smooth on throat where the presence of a single vocal sac is clearly recognizable. Femoral glands very poorly delimited and very indistinct from both external and internal views; a patch of 16 small granules are visible from internal view.

Colouration dorsally brownish, slightly lighter on the back and head in an area delimited by the dorsolateral folds. Limbs light brown with brown crossbands: three to four bands on forelimb, four to five on femur, four to six on tibia, five to six on foot and tarsus. Flanks brown fading into cream towards the belly. Head laterally brown, with a distinct horizontal dark brown stripe running underneath the canthus rostralis and the supratympanic fold. Two light vertical stripes run from underneath the eye to the upper lip. Lower lip brown with five narrow light vertical markings. Ventrally brownish with irregular light mottling on the throat (vocal sac), cream on the remaining surface, with brown mottling in the breast region and on the hindlimbs.



Fig. 9. Female paratype (ZSM 937/2000) of *Mantidactylus tandroka*, spec. nov. from Marojezy in life (ventral view).

Colour in life. Colour slides of living specimens are only available of the female paratype ZSM 937/2000 (Figs 8-9). The dorsal colouration was light brown to beige, the flanks were light brown fading into pinkish towards the venter. The limb crossbands were greyish brown. A black stripe below the canthus rostralis from snout tip to eye and below the supratympanic fold. Tympanum dark brown. The iris was light yellowish brown in its upper third, dark reddish brown in its two lower thirds. The pupil was horizontal. The venter was partly transparent with a pinkish shade, more cream coloured in its posterior part and on the hindlimbs. The throat was dirty white and unspotted.

Variation. Morphologically, the paratypes agree well with the holotype. The general impression of a broad and relatively short head is very typical in all available specimens. Two specimens (MNHN 1973.927-928) show light stripes from snout tip along canthus rostralis and above eye. These stripes become broader immediately behind the eyes and along the supratympanic fold, making up the entire flank colouration from the forelimb insertion on. The distinct and sharp colour border between light flanks and dark dorsum is situated slightly below the dorsolateral folds. A similar pattern is known in *M. redimitus* and *M. cornutus* and described above for one *M. tschenki* paratype. In these species, however, the light colour on the flanks is less extended. The expression of this pattern thus may constitute another relevant diagnostic character of *M. tandroka*. The male MNHN 1973.926 shows very distinct broad cream-white vertical bands running from the anterior and the posterior eye corners to the upper lip, respectively, reminding the pattern found regularly in *M. leucomaculatus*. Generally, in most preserved specimens (also in the females ZFMK 59894, although not in the figured specimen ZSM 937/2000; Figs 8-9) the throat shows an intense brown pattern, as opposed to the greyish colour in *M. redimitus*, *M. cornutus*, and *M. tschenki*. As far as visible in the preserved males the vocal sac is single subgular although a slightly bilobed shape as in *M. tschenki* can not be excluded before observations of calling males become available. Altogether, male SVL in the type series was 38.7-41.4 mm (39.3 ± 1.2 mm, $n=5$), female SVL 39.6-44.7 mm (41.8 ± 2.2 mm, $n=5$). Mean male size was 94 % of mean female size, sexual size dimorphism was statistically significant (U-test, $P < 0.05$). Mean relative tympanum size did not differ significantly between sexes (U-test, $P > 0.9$), while intersexual differences in

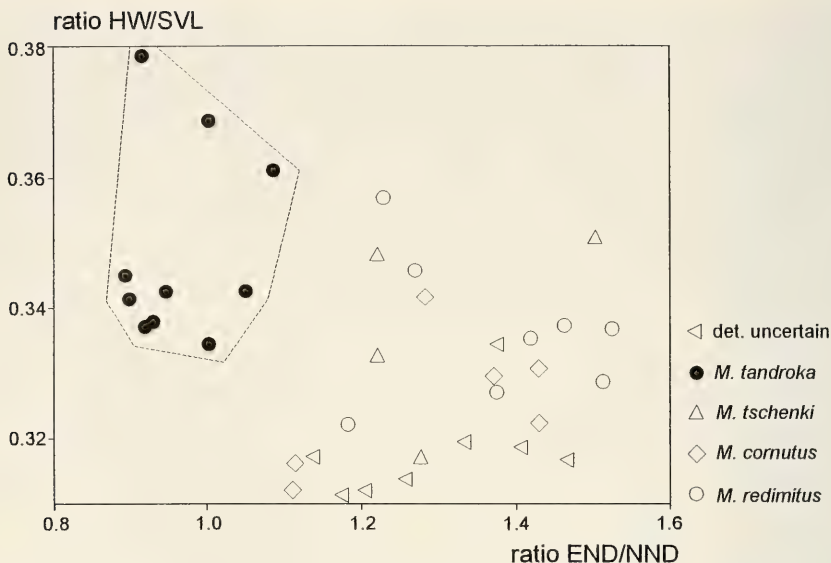


Fig. 10. Scatterplot of HW/SVL ratio vs. END/NND ratio in *Mantidactylus tandroka*, *M. cornutus* and *M. tschenki*, and *M. redimitus* showing separation of *M. tandroka* from the remaining specimens by head shape parameters.

relative length and height of inner metatarsal tubercle (means of both values larger in males) were significant (U-test, $P < 0.05$).

Habitat and habits. ZFMK 59894 and ZSM 937/2000 were collected during the day on the ground in primary rainforest. Advertisement calls are unknown.

Distribution. *Mantidactylus tandroka* is only known from the type locality, around 1300 m altitude.

Etymology. Derived from *tandroka* (Malagasy: horn), referring to the two horn-like tubercles between the eyes of this and related species (see also the etymology of *M. cornutus*). The name is considered as invariable noun standing in apposition to the generic name.

Relationships. *Mantidactylus tandroka* appears most closely related to *Mantidactylus cornutus* and *M. tschenki*.

Subgeneric attribution. *Mantidactylus tandroka* is included in the subgenus *Phylacomantis* Glaw & Vences, 1994 based on its similarity to *M. cornutus* and *M. tschenki*.

Discussion

Vouchers of uncertain attribution. When preserved, *M. cornutus* and its new sibling species *M. tschenki* are virtually indistinguishable by morphological characters. Therefore, the identity of specimens from four localities (Ranomafana, Andringitra, Col Ivohibe, and Chaines Anosyennes) attributed in Glaw & Vences (1994) to *M. cornutus* is uncertain and commented as follows: (1) The Ranomafana specimen (ZFMK 50593) was defined as paratype of *M. cornutus* by Glaw & Vences (1992b). It is a female of rather large SVL (40.7 mm) in comparison to the four available specimens of *M. tschenki* (all males). Despite of this size difference, it may belong to *M. tschenki*, but further fieldwork is necessary to confirm or reject the presence of both species in the Ranomafana area. (2) The specimens from the Chaines Anosyennes, Campsite 4 (MNHN 1972.1471) and Chaines Anosyennes, Ambana (MNHN 1972.1472) are two males in good state of preservation which are larger than the available specimens of *M. tschenki*; furthermore they have a pair of distinct tubercles on the central dorsum lacking in *M. tschenki* (but present in the Ivohibe specimens). (3) The three specimens from Col d'Ivohibe, 1400 m altitude (MNHN 1953.74, 1991.2940-2941) are in mediocre state of preservation but agree better with *M. cornutus* than

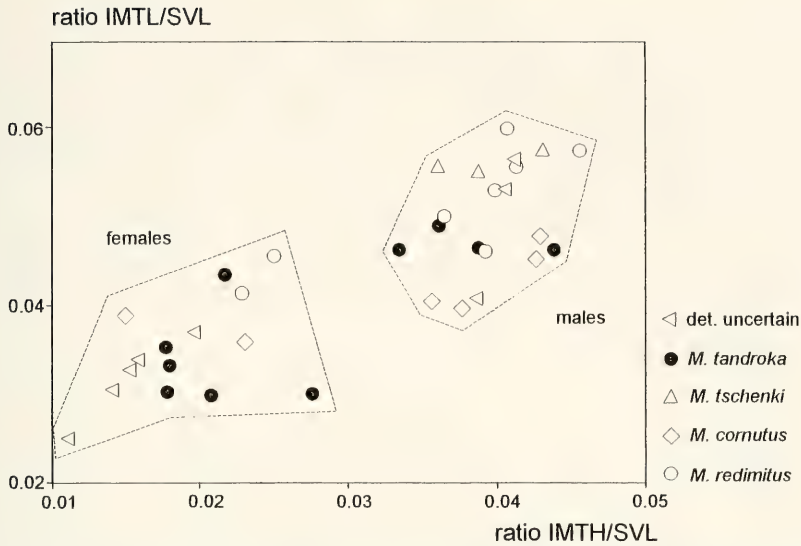


Fig. 11. Scatterplot of relative length and height of the inner metatarsal tubercle (ratios IMTL/SVL and IMTH/SVL) in *Mantidactylus redimitus*, *M. cornutus*, *M. tschenki*, and *M. tandroka*, showing sexual dimorphism in IMT size. Original measurements from Tab. 1 (except type of *M. redimitus*).

M. tschenki regarding body size. (4) The two Andringitra specimens (MNHN 1972.571-572) are rather small and in bad state of preservation; they are females, and it can not be verified whether they are actually full-grown adults (only immature oocytes observed after dissection). Summarizing, more fieldwork is necessary to clarify the identity of these four populations.

Distribution pattern in *Phylacomantis*. Although one of the new species described in the present paper (*M. tschenki*) is only known from south-eastern Madagascar, the new data which have been gathered during the last years clearly show that the subgenus *Phylacomantis* has its center of diversity and endemism in northern Madagascar which together make up less than 1/5 of the Malagasy territory. Including a further new *Phylacomantis* species from the central east (Andasibe) and Marojezy which is being described elsewhere, only three out of nine *Phylacomantis* species (*M. cornutus*, *M. tschenki*, *M. corvus*) are not known from northern Madagascar and three species appear to be northern endemics (*M. granulatus*, *M. pseudoasper*, *M. tandroka*). The highest diversity is found in the Marojezy massif where six species occur: *M. redimitus*, *M. tandroka*, *M. leucomaculatus*, *M. granulatus*, *M. pseudoasper*, and the new species which is being described in a separate paper. This high degree of sympatry is in part characterized by a restricted altitudinal distribution at Marojezy (e.g. *M. tandroka* to the high elevations above 1000 m, *M. granulatus* mainly at low altitudes). Such an altitudinal segregation may be one factor favouring the extraordinary anuran diversity in Madagascar and the high degree of range overlap among closely related species.

Shared characters in *Phylacomantis*. The new morphological and bioacoustic data presented allow for the discussion of some general trends in the subgenus *Phylacomantis*. In two species in which males and females were available (*M. redimitus*, *M. tandroka*), a sexual dimorphism in size of the inner metatarsal tubercle was noted, males having distinctly larger tubercles than females. Actually, no overlap between males and females was noted even pooling the data of all four species studied (Fig. 11). Beside the two mentioned species, the sexual dimorphism of inner metatarsal tubercle within the genus *Mantidactylus* is only known in *M. granulatus* and *M. leucomaculatus* (Glaw & Vences 1994) and some species of the subgenus *Gephyromantis* (pers. obs.), and may be a synapomorphy of this group of species. On the other hand, sexual dimorphism in tympanum size appears to be absent in the species studied here. Such a dimorphism is typical for several *Mantidactylus*, especially species in the brook edge dwelling subgenera (e.g. *Brygoomantis*, *Chonomantis*, *Ochthomantis*), and is also found in *M. pseudoasper* (Glaw & Vences 1994), a member of the subgenus *Phylacomantis*.

There is one other character which seems to be restricted to several species of the subgenus *Phylacomantis* and to some members of the subgenus *Gephyromantis*: The laterally banded morph is only known to occur in *M. redimitus*, *M. cornutus*, *M. tschenki* and *M. tandroka* (*Phylacomantis*), as well as in *M. asper* and *M. luteus* (*Gephyromantis*) (pers. obs.). All four mentioned *Phylacomantis* species have also dermal spines above the eye, a character shared with another undescribed *Phylacomantis* species, some species of the subgenus *Gephyromantis* (*M. asper*, *M. spinifer*), and species of the subgenus *Spinomantis* (e. g. *M. phantasticus*).

Advertisement calls of *Phylacomantis*, as far as known, are composed of a single note type, although notes can be arranged in groups. The four species studied here share with each other and with *M. granulatus* and *M. leucomaculatus* calls with further structural similarities: They consist of rather regular series of unharmonious notes with a note duration of at least 50 ms and a pulsed structure, possibly reflecting relationships between these species which were placed in a *M. granulatus* group by Glaw & Vences (1994).

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